COMPARATIVE STUDY OF THE GILL AREA OF MARINE FISHES

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Among fishes there are obvious species differences in number of gill arches, as well as in number and length of gill filaments. Less obvious are species differences in number and size of the respiratory units, the gill lamellae. This suggests that there is also variation in gill surface area per unit of size of fish. Since fishes occupy a variety of ecological niches it is of interest to know if the gill area may in any way be correlated with activity and habitat.

Although there have been many studies on the anatomy of fish gills, only a few investigators have concerned themselves with gill area. Riess (1881) was among the first to attempt accurate measurements of gill surface. He found that pike had 125 sq. mm. of respiratory surface per gram of body weight. Putter (1909) determined gill surface area of a few fishes, particularly *Scorpaena*, and felt that the respiratory surface was proportional to body surface but not to body weight as maintained by Riess. The most extensive study on a single species was made by Price (1931), who followed the changes in gill area throughout the development of small-mouthed bass. The only study of a comparative nature appears to be that of Schöttle (1931), who found a reduction of gill surface in terrestrial gobiiform fishes compared to strictly aquatic species.

The studies reported here were carried out exclusively on marine teleost fishes repr^esenting twenty-three families and thirty-one species. The work was done in part at the Marine Biological Laboratory, Woods Hole, Mass., and in part at the Duke University Marine Laboratory, Beaufort, N. C. Partial support came from the Duke University Research Council.

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METHODS

Each gill filament is made up of numerous respiratory units, the lamellae or platelets. To obtain the respiratory area of a fish it is necessary to know the total area of the lamellae. It is, of course, impractical to measure each of the thousands of lamellae present; consequently a sampling method must be employed.

After weighing the fish and making outline drawings for later determination of body surface area, the gill arches of one side were dissected out, carefully separated, and placed in dishes of sea water, one arch to each dish. The number of filaments on each side of each arch was counted under a dissecting microscope. The average length of the filaments was determined by measuring every tenth filament with vernier calipers. From these measurements the average length of the filaments was established. By placing filaments of approximately average length under the low power objective of a compound microscope and using either a stage or an ocular micrometer, the number of lamellae per millimeter of filament was determined. What appeared to be lamellae of average size were separated from filaments of average size and placed on slides. Camera lucida drawings were then made of several lamellae. Usually this could be done using the lower power objective of a compound microscope. Planimeter readings were made of the camera lucida drawings and an average taken.

Knowing the number of gill filaments, the average length of the filaments, and the number of lamellae per millimeter of filament, the total number of gill platelets was readily determined. From this and the known magnification and area of the camera lucida drawings, the total area of gill surface could be computed.

In those species with extremely delicate filaments, the task of obtaining undamaged platelets was facilitated by hardening the filaments for a few minutes in formaldehyde or Bouin's fluid. The central cartilaginous support of the filament that runs through each lamella was not included in the computation of area. Since the lamellae are functional on both sides the determined area was doubled.

Admittedly, with so many manipulations, there is a large possibility of error in determining gill area. However, all specimens were treated in the same manner so that the results obtained would be comparable.

Body surface area of most species was found by drawing around the fish, allowing for body thickness and omitting dorsal, anal and paired fins, and determining the area of the outline with a planimeter. This method is quite adequate for depressed and compressed fishes, such as goosefish and butterfish. It can be used with more difficulty with odd-shaped fishes like sea robins, puffers, and toadfish. The body surface areas of these latter species were also determined by the more laborious method of covering the body with pieces of paper and making planimeter readings on each piece. The use of a general formula for determining body surface area was discarded because the different species differed in form and weight and a correction factor for each species would first have to be obtained. This has been discussed in a previous paper (Gray, 1953).

Results and Discussion

In Table I, which includes 31 species representing 23 families of marine teleosts, it can be clearly seen that species differ widely in number of respiratory lamellae and in respiratory area. This is true whether comparison is based on unit of body weight or on unit of body surface. In this table species are arranged in descending order of gill area per square centimeter of body surface. The contrast in respiratory area of those species near the top when compared with those near the bottom is great. One familiar with common marine fishes of the Atlantic coast will see a general correlation between respiratory area and species activity.

For convenience of discussion, and with no sharp demarcation between them, the fishes may be divided into three groups.

I. Active, schooling, migrating, fast swimming, streamlined fishes that, at least in the adult stage, seldom frequent the smaller estuaries. To this group clearly belong the mackerels, menhaden, dolphin, bluefish. At least during the summer months these species are in constant motion as they feed on plankton or follow schools of smaller fish.

II. Fishes of moderate activity, estuarine species limited in their daily travels. These include such species as scup, sheepshead, sea bass and others that hang around jetties, wrecks, piers, etc., feeding on crustaceans, molluscs, and sessile animals. On the lower fringes of this group may be included tautog, sea robins and puffers that spend part of their time resting on the bottom.

III. Relatively sluggish species more or less adapted for benthic life. Toadfish, goosefish, and flounders are good examples.

TABLE I

Gill area of marine fishes

Species of fish	No. of determinations	Average weight (gms.)	Lamellae per mm. of filament	Gill Area (sq. mm.)					
				Per gram of body weight			Per sq. cm. of body surface		
				max.	min.	ave.	max.	min.	ave.
False albacore, *Gymnosarda alleterata*	1	5216	33	1939	1939	1939	4854	4854	4854
Menhaden, *Brevoortia tyrannus*	12	613	29	2547	1241	1773	2704	1300	1828
Dolphin, *Coryphaena hippurus*	4	4015	26	965	618	710	1334	971	1169
Bonito, *Sarda sarda*	2	2192	31	631	558	595	1237	1073	1155
Bluefish, *Pomatomus saltatrix*	1	1035	29	652	652	652	841	841	841
Common mackerel, *Scomber scombrus*	15	182	31	1532	802	1158	1103	543	838
Spanish mackerel, *Scomberomorus maculatus*	2	478	29	770	768	769	731	724	728
Jumping mullet, *Mugil cephalus*	9	166	27	1105	760	954	845	538	654
Hard tail, *Caranx crysos*	3	129	39	1048	894	982	610	567	594
Striped bass, *Roccus lineatus*	4	3059	19	426	148	302	818	415	592
Sheepshead, *Archosargus probatocephalus*	6	2366	19	467	212	328	553	333	488
Bur fish, *Chilomycterus schoepfi*	2	316	13	449	425	437	492	482	487
Scup, *Stenotomus chrysops*	7	395	26	623	391	506	612	352	478
Tautog, *Tautoga onitus*	6	580	18	519	293	392	531	317	435
Red-winged sea robin, *Prionotus strigatus*	11	460	20	768	318	483	642	191	424
Butterfish, *Poronotus triacanthus*	9	199	31	817	386	598	572	252	411
Sea trout, *Cynoscion regalis*	6	807	27	593	221	373	671	253	410
Rudderfish, *Palinurichthyes perciformis*	6	199	24	658	377	506	550	268	388
Remora, *Echeneis naucrates*	2	393	22	783	314	549	—	—	—
Puffer, *Spheroides maculatus*	13	250	16	956	324	470	585	232	372
Sea bass, *Centropristis striatus*	4	244	21	653	439	458	480	233	361
Goosefish, *Lophius piscatorius*	3	6392	11	267	116	196	360	245	299
Harvest fish, *Peprilus alepidatus*	2	71	26	526	483	505	257	230	244
Conger eel, *Leptocephalus conger*	2	2560	19	136	134	135	224	202	213
Brown sea robin, *Prionotus carolinus*	2	213	20	394	326	360	225	197	211
Cutlass fish, *Trichiurus lepturus*	3	116	31	627	361	536	244	138	198
Common eel, *Anguilla rostrata*	4	428	19	398	183	302	236	125	193
Fluke, *Paralichthys dentatus*	5	766	19	328	206	242	225	134	176
Flounder, *Pseudopleuronectes americanus*	2	734	18	218	183	200	134	115	125
Toadfish, *Opsanus tau*	58	233	11	362	94	197	226	69	125
Sand flounder, *Lophopsetta maculata*	1	411	20	188	188	188	90	90	90

The numbers of lamellae per mm. of gill filament are also included in Table I. Here again it is found that, in general, the most active fishes have smaller lamellae placed closer together than do the more sluggish species. Usually a large number of small lamellae means more surface than a small number of large lamellae. But of course other factors such as the length of the filaments, the number of filaments and the number of gills are also important in determining the amount of gill surface.

Fishes with large lamellae spaced far apart often live longer out of water than those with closely packed fine lamellae. A toadfish will live for hours on the laboratory floor; a butterfish dies in a matter of minutes. Delicate closely spaced lamellae adhere together when removed from an aquatic medium and the functional surface is thus greatly reduced. It is the sluggish fishes with low metabolism that have the widely spaced lamellae.

In gobies, Schöttle (1931) has shown that those capable of remaining out of water have gill lamellae so arranged as not to collapse when the fish is on land.

Criteria for estimating degree of activity are unfortunately not based on oxygen consumption. It is desirable but difficult to obtain comparative metabolism data on marine fishes. From necessity most data are obtained from sluggish and moderately active species. Active species are hard to keep in captivity, or even to get to the laboratory, without becoming partially asphyxiated. Some, and this has been observed particularly in the family Scombridae, apparently die quickly from nervous exhaustion. This is especially true of schooling fishes when separated from their companions. However, the fact that it is difficult to maintain these fishes in the

TABLE II

Order of rank of marine fishes based on number of lamellae and on gill area

Gill lamellae per mm. of filament		Gill area per gram of body weight (sq. mm.)		Gill area per cm. of body surface (sq. mm.)	
1. Mackerel	31	1. Menhaden	1773	1. Menhaden	1828
2. Butterfish	31	2. Mackerel	1158	2. Dolphin	1169
3. Menhaden	29	3. Mullet	954	3. Mackerel	838
4. Mullet	27	4. Dolphin	710	4. Mullet	654
5. Sea trout	27	5. Butterfish	598	5. Striped bass	592
6. Dolphin	26	6. Scup	506	6. Sheepshead	488
7. Scup	26	7. Rudderfish	506	7. Scup	478
8. Rudderfish	24	8. Sea robin	483	8. Tautog	435
9. Sea bass	21	9. Puffer	470	9. Butterfish	429
10. Sea robin	20	10. Sea bass	458	10. Sea robin	424
11. Striped bass	19	11. Tautog	392	11. Sea trout	410
12. Sheepshead	19	12. Sea trout	373	12. Rudderfish	388
13. Eel	19	13. Sheepshead	328	13. Puffer	372
14. Fluke	19	14. Striped bass	302	14. Sea bass	361
15. Tautog	18	15. Eel	302	15. Eel	193
16. Puffer	16	16. Fluke	242	16. Fluke	176
17. Toadfish	11	17. Toadfish	197	17. Toadfish	125

laboratory is at least a qualitative indication of relative activity even though not a quantitative one. It is these species that have the greatest relative gill surface.

Researches of others on some of the same species lend support to the theory that the active fishes have higher metabolism than bottom dwellers. Hall and Gray (1929) in their hemoglobin studies showed that the mackerel with 43 and the menhaden with 41 were relatively high in mgs. of iron per 100 cc. of blood, in contrast to the goosefish with 14.7, toadfish, 13.5, and sand flounder, 11.5. Scup (25.3), sea robin (23.7), and puffer (21.5) were intermediate. Also, Hall and McCutcheon (1938) have pointed out a correlation of hemoglobin function with activity and habitat in marine fishes. Mackerel and toadfish represented the extremes of the fishes they studied, with scup occupying an intermediate position.

Similarly, Gray and Hall (1930) showed that active fishes had greater amounts of blood sugar per 100 cc. of blood than did less active species (menhaden 75 mgs., mackerel 64, scup 53, sea robin 37, puffer 23, toadfish 15, and goosefish 6).

Vernberg and Gray (1953) found that a correlation exists between oxygen consumption of excised brain tissue and activity in fishes. The O_2 consumption of menhaden brain was found to be nearly twice that of toadfish brain, with moderately active fishes occupying an intermediate position.

Thus it seems that there are many correlations with activity and it is not surprising that there should also be a correlation between gill area and activity.

A just criticism of Table I could be that in many cases only one or two determinations were made and with the possibility of such a large potential experimental error there might arise a question of accuracy. However, if we consider only the seventeen species for which four or more determinations were made, there still remains a definite correlation with activity. This is shown in Table II where rank in order of number of lamellae per mm. of filament, gill area per gram of body weight and gill area per square centimeter of body surface are given. The order shifts a little in the three columns but the principle still holds: active fishes in general have more lamellae per mm. of filament, and greater respiratory area per unit of weight or per unit of body surface.

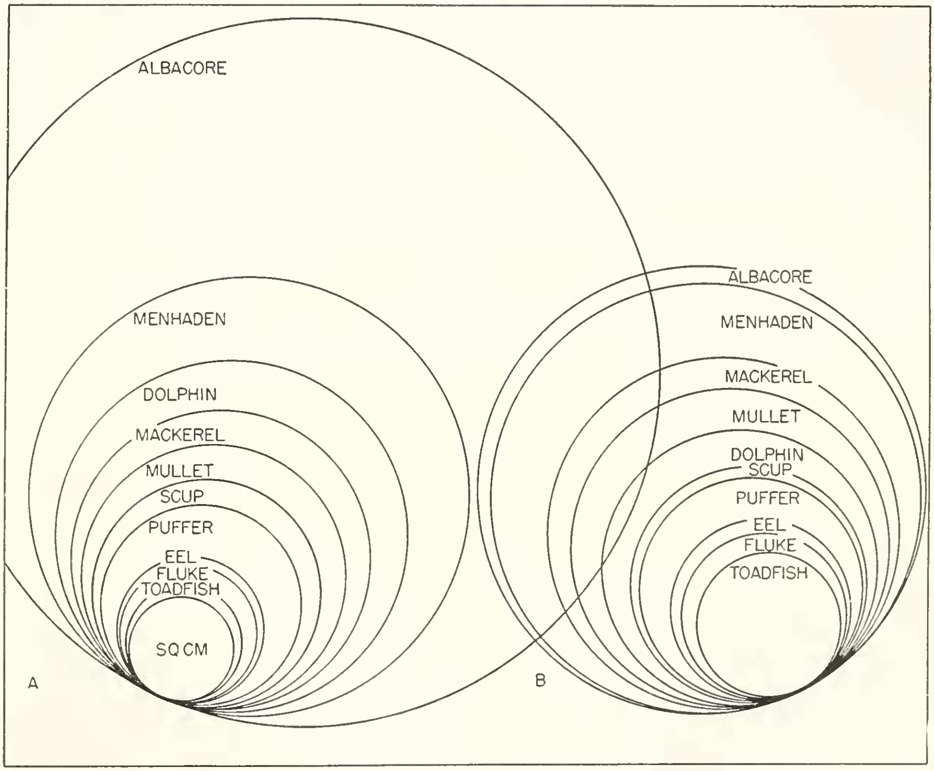

FIGURE 1. Relative gill areas of marine fishes. A. Per sq. cm. of body surface area. B. Per gram of body weight.

A more serious criticism is that the fish studied are not of the same size. This is especially significant when using body surface area as a basis for comparison, for a large fish has a relatively smaller body surface area in proportion to body weight than does a smaller fish of the same species. At first glance, the respiratory area of the false albacore per square centimeter of body surface may seem out of line. Unfortunately only one determination was made so that there can be only speculation as to accuracy. However, the surface area of this fish was in line with that of other scombrids (Gray, 1953), and gill area determinations were rechecked. This is a muscular, fast swimming fish with relatively small body surface area and it is to be expected that the ratio of respiratory area to body surface area would be high. Attempts to obtain gill areas of larger ocean fishes such as tuna were in vain. If one may be permitted to speculate, the prediction is that when obtained, the respiratory area of a large tuna in relation to body weight will be found to be near that of the albacore, but will exceed that of the albacore by many times when compared to body surface area.

Table III

Respiratory area of fishes of the same weight

Fish	Weight (gms.)	Total gill area (sq. mm.)
Menhaden	540	821,079
Sheepshead	544	254,237
Tautog	547	198,201
Toadfish	560	72,871
Menhaden	620	858,322
Toadfish	620	86,867

Figure 1 shows graphically the relative gill area of several species of teleost fish, representing different degrees of activity, compared both on the basis of unit of body surface (A) and on unit of body weight (B). The false albacore illustrates clearly the difficulty in comparing fishes of vastly different sizes on the basis of body surface. This streamlined fish was not only much larger than the others but also had an extremely large gill area. It seems to the author that when comparing gill areas of fishes of different species and differing greatly in size the comparison is more satisfactorily made when based on unit of weight than on unit of body surface area. Certainly the weight can be obtained much more easily and accurately than can body surface area.

Table III shows that when fishes of approximately the same weight are compared there is a definite species difference in respiratory area. It is seen here that the respiratory area of the active menhaden is roughly ten times that of the sluggish toadfish of the same weight, and that the moderately active sheepshead and tautog occupy an intermediate position.

Summary

1. The gill areas of 31 species of marine teleost fishes have been compared.

2. Active, fast swimming, schooling, streamlined fishes (such as menhaden, mackerel, bluefish) have relatively much greater gill areas than do sluggish, benthic

species (toadfish, goosefish, flounders). Fishes of moderate activity (scup, sheepshead, sea bass, sea robin, puffer) are also intermediate in gill area.

3. Species differences in gill area exist whether comparison is based on unit of body surface area or on unit of body weight.

4. In general benthic fishes have fewer gill lamellae spaced farther apart than do fast swimmers.

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